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# Lateglacial vegetation development in Denmark – New evidence based on macrofossils and pollen from Slotseng, a small-scale site in southern Jutland

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ABSTRACT

This paper presents the first unambiguous terrestrial palaeoecological record for the late glacial "Bølling warming" in Denmark. Pollen and macrofossil stratigraphies from pre-Bølling to 10,800 cal yr BP are presented from a small kettle hole in Southwest Denmark, during which the lake basin developed from an immature stage after the deglaciation to complete infilling in the early Holocene. Results show that the recently deglaciated landscape bore a discontinuous vegetation of pioneer plants. After the Bølling warming, an open *Dryas octopetala-Betula nana* community developed with *Helianthemum oelandicum*. Subarctic species were dominant and local successions were probably delayed by relatively unstable and infertile soils. There is no indication of a climate cooling during the period corresponding to the Older Dryas, but the occurrence of several drought tolerant and steppe species indicates that the period was relatively dry. In the Allerød period the *Dryas-B. nana* vegetation was initially replaced by an open *Salix* and grass dominated vegetation and some 400 years later, the first tree birches were documented presumably occupying moist and sheltered soils while drier land remained open. In the Younger Dryas period trees disappeared and the vegetation became open again and dominated by subarctic species. Following climate warming at the Younger Dryas–Holocene transition a shrub community of *Empetrum* and *Juniperus* developed. After approximately 200 years it was replaced by birch forest. Overall, the late-glacial vegetation cover had a more open and patchy character than inferred from previous pollen studies as assessment of the vegetation succession based on macrofossil evidence is essential. The inferred general vegetation development corresponds well with results of other studies in the region. Canonical ordinations (RDA) indicate that vegetation changes at the landscape scale during the Lateglacial period were driven by changes in climate, soils and competition for light.

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## 1. Introduction

The late glacial vegetation development in northwestern Europe has drawn the attention of palaeobotanists and palaeoecologists for more than a century. From numerous pollen records a well established interpretation of the vegetation development in relation to climate, soil development, natural succession etc. had already emerged by the mid 20th century in Denmark and south Sweden (e.g. Iversen, 1954; Berglund, 1966). Within recent years, however, macrofossil-based reconstructions have helped to shape a more detailed and partly unexpected picture of late-glacial environmental development in southern Sweden (Jönsen, 1988) and western Norway (Birks, 1993, Van Dinter and Birks, 1996; Birks et al., 2000; Birks et al., 2005; Birks, 2003). One of the primary advantages in using macrofossils for palaeoenvironmental reconstructions is their high taxonomic precision and their local origin which give valuable insights into the local environments not normally attainable through pollen records alone. Although late-glacial palaeoecological studies started with plant macrofossil records (e.g.

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Nathorst, 1871; Hartz and Milthers, 1901; Jessen, 1920) the number of macrofossil-based reconstructions covering this period is still few compared to the large number of pollen studies. This is unfortunate since macrofossil-based reconstructions often show a more diverse and multifaceted development than recorded by pollen analysis (e.g. Birks, 1993, 2001, 2007; Birks and Birks, 2000; Walker et al. 2003; Bos et al. 2006; Hofstetter et al. 2006; Jackson and Booth, 2007). Discrepancies between pollen and macrofossil based-reconstructions are partly related to the facts that sedimentary pollen assemblages are influenced by changes in source area and vegetation patchiness as well as pollen production and that they suffer from limited taxonomic precision (Prentice, 1985; Sugita, 1994; Nielsen and Sugita, 2005; Jackson and Booth, 2007). This is especially pronounced in treeless arctic environments where only a limited proportion of the sedimentary pollen may be of local origin (see Birks and Birks, 2000). An example of the discrepancy between pollen and macrofossil-based reconstructions is the pattern of inferred tree-birch expansion during the late glacial. Often a significant time lag is recorded in the presumed local appearance of birch trees based on pollen records and that based on macrofossil records. This discrepancy is probably caused by high proportions of long distance transported pollen into vegetation with low pollen production (Birks, 1993, Van Dinter and Birks, 1996; Bennike et al. 2004a). Another example is the frequent occurrence of "no-analogue" pollen assemblages from late-glacial deposits, which are traditionally interpreted as deriving from plant communities having no present day match (Jackson and Williams, 2004). Such "no analog" pollen assemblages are, however, not very often accompanied by "no analog" macrofossil assemblages (Birks, 2003), again pointing at the difficulties in differentiating between local and regional signals in pollen records. These inconsistencies between pollen and macrofossil assemblages can cause uncertainties in the vegetation reconstruction (Birks, 2003; Birks et al., 2005). This has potentially large consequences because vegetation and climate reconstruction are used for interpreting the mechanisms of past climate changes and for validation of palaeoclimate models (e.g. Isarin and Bohncke, 1999; Renssen and Isarin, 2001). Improved understanding of the relation between macrofossil and pollen assemblages is, therefore, important in order to get a more precise picture of the vegetation development during the late glacial. The two methods complement each other.

In Denmark, lake deposits containing undisturbed biostratigraphies of the late-glacial development prior to the Allerød warming are surprisingly rare. In fact, no unequivocal Danish terrestrial bio- and chronostratigraphy was known for the period 15,000–14,000 cal yr BP until the discovery of the Slotseng locality (Mortensen, 2007). Slotseng, a small kettle hole next to a palaeolithic settlement, was excavated in 2000 and 2001 by the National Museum of Denmark. In the lake deposits, flint implements and the remains of at least eleven reindeer killed by palaeolithic hunters were documented (Holm, 1993; Holm et al. 2002; Aaris-Sørensen et al. 2007). The flint type belongs to the Havelte phase of the Hamburgian culture. Typologically dated to the late Bølling/Older Dryas period, they are the oldest firm evidence of human presence in Denmark (Holm et al. 2002). Besides this unique archaeological context the kettle hole revealed a well preserved, partly organic sediment sequence covering the period from pre-Bølling to early Holocene. During the excavation the deposits from the entire basin were exposed in an open profile allowing a detailed study of the basin stratigraphy, morphology and development (Fig. 2, Mortensen, 2007). On the basis of macrofossil, pollen, and physical analyses of these sediments, this paper aims to 1) describe the local vegetation development within the lake and the lake catchment, 2) identify possible no-analogue assemblages in macrofossil and pollen records, and 3) discuss local vegetation responses in relation to climatic and environmental changes.

## 2. Study area

The Slotseng site is located just east of the main stationary line of the Weichselian glaciation in southwest Denmark within the former glaciated area (55°19`43"N/9°16`8.24"E) 40 m a.s.l. (Fig. 1).

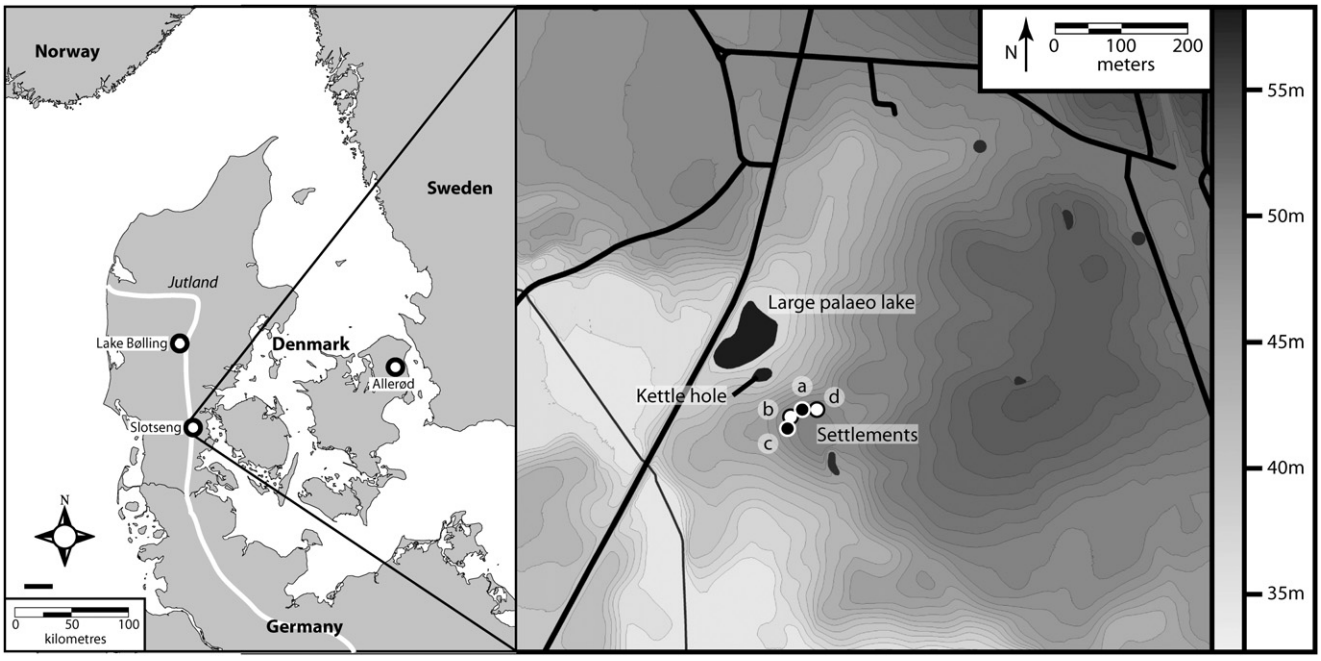


**Fig. 1.** Location of Slotseng in SE Jutland showing the main stationary line of the Scandinavian Ice sheet during the Weichselian. Besides the Slotseng locality, Bølling and Allerød *loci classici* are shown. The small map shows the local topography of the Slotseng area with the location of the kettle hole, the larger lake and the settlements of the Hamburgian and Federmesser cultures. Contour equidistance is 50 cm.

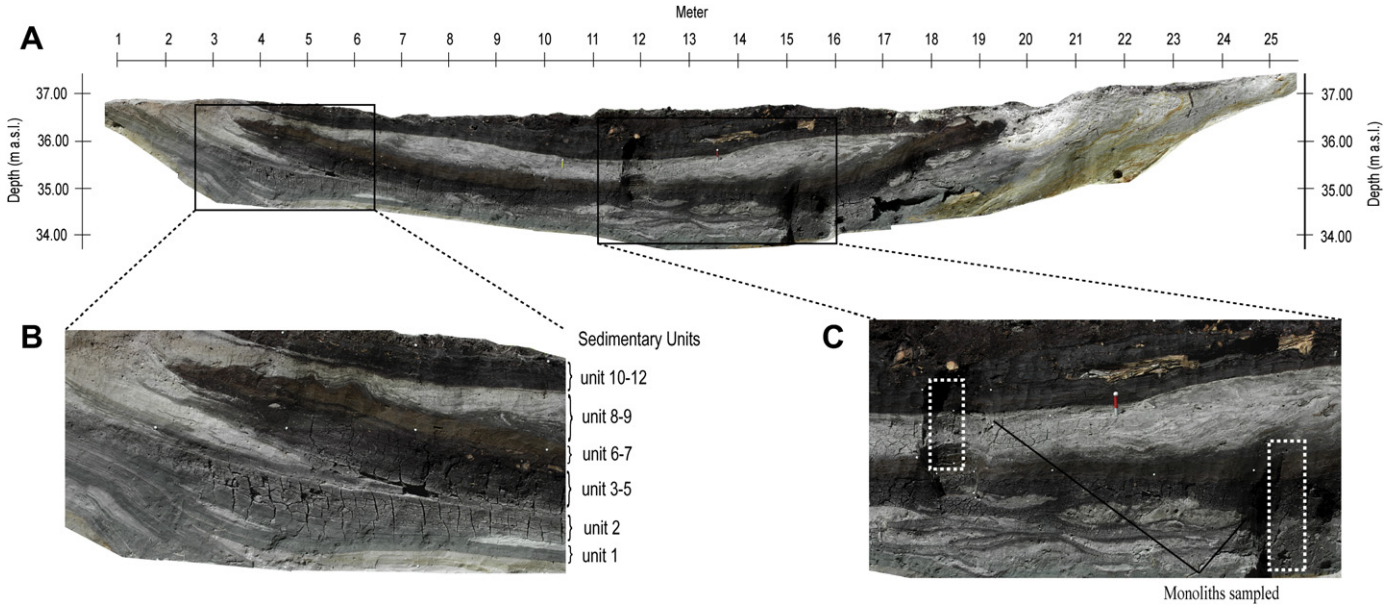


**Fig. 2.** Orthogonal photograph of the transect of the Slotseng kettle basin showing the stratigraphy and monoliths sampled.

The mean temperature of the area today is: annual 8.2 °C, January 1.3 °C, July 16.4 °C and annual precipitation is 864 mm (Theilgaard, 2006). During the Weichselian glaciation the Scandinavian Ice Sheet reached its maximum extent across Denmark about 22,000 cal yr BP, covering all except for the western part of Jutland (Houmark-Nielsen and Kjær, 2003). The main stationary line, a terminal moraine landscape, formed the Jutland ridge, which later became the major watershed divide in Jutland and an important immigration route for animals and ultimately Man (Jensen, 2001). Around 19,000 cal yr BP the ice sheet had receded leaving a slightly undulating dead-ice landscape of calcareous tills to the east and an extended outwash plain to the west of the main stationary line (Houmark-Nielsen and Kjær, 2003).

South of the former lake at Slotseng is a small kettle-hole basin, now filled in, with an area of approximately 0.05 ha. This former lake was closed, c. 25 m wide and maybe a few meters deep. Today the area is part of extensive farmland, the wetland deposits being covered by colluvial soil.

## 3. Material and methods

### 3.1. Stratigraphy

During the archaeological excavation the deposits were exposed in an east-west transect through the whole basin (Fig. 2). This allowed a detailed study of the sediment stratigraphy and an exhaustive lithological log was made using the Troels-Smith system (1955). Despite a rather complex pattern of sedimentation affected by melting of dead ice, water-level changes, slumping, erosion, and ice rafting of sediment, parts of the basin contain an undisturbed stratigraphy. In these parts, as close to the centre of the basin as possible, two monoliths were sampled covering a total of 2.18 m of late glacial and early Holocene deposits (excluding the overlapping section) (Fig. 2). Their depths are recorded as metres above sea level (m a.s.l.). The monolith field description was supplemented by laboratory observations and by percent loss on ignition (LOI) and magnetic susceptibility (SUS). These analyses were made on continuous samples of 1 cm. For LOI, 2 $cm^3$ samples were weighed, dried, ignited at 550 °C for 8 h, and weighed again. SUS was measured using c. 1 g of dry sediment with a KLY-2 susceptibility-meter capable of reaching c. $1x10^{-6}$ SI-units.

### 3.2. Radiocarbon analysis (calibration, age-depth model)

#### 3.2.1. $^{14}C$ dating

In 2002, AMS $^{14}C$ measurements of 18 samples of terrestrial material, mainly *Salix* twigs, were made from the lower part of the sequence (Table 1). In 2005 material from 14 additional levels sampled during macrofossil analysis, was dated. The material had been stored in a refrigerator. Strictly terrestrial plant macrofossils were dated (e.g. deciduous leaf-fragments and fruits were used, or twigs in the absence of the former) (Table 1). Plant remains, in which incorporation of old carbon cannot be excluded e.g. from wet habitat plants such as *Carex* sp. and *Typha* sp., were excluded. Material for $^{14}C$ determination was secured from within the 1 cm contiguous samples and was subjected to a standard base-acid-base treatment to remove possible contaminants, such as carbonates and infiltrating humics. The dating results are reported according to international conventions (Stuiver and Polach, 1977) as conventional $^{14}C$ dates in $^{14}C$ yr BP (before AD 1950) based on the measured $^{14}C/^{13}C$ ratio corrected for the natural isotopic fractionation by normalizing the result to the standard $\delta^{13}C$ value of $-25‰$ VPDB (Andersen et al. 1989). Dates were calibrated and an age-depth model was constructed using OxCal 4.1 (Ramsey, 2008) using the radiocarbon calibration curve IntCal04 (Reimer et al. 2004). The mean age of 10 reindeer bones embedded in the sediments between 34.74 and 34.78 m a.s.l. (Mortensen, 2007) was compared with the model (Fig. 3).

### 3.3. Pollen analysis

Of a total of 218 contiguous samples 66, each comprising 1 $cm^3$, were chosen for pollen analysis (Figs. 4 and 5). An exotic marker (*Lycopodium*) was added for estimating pollen concentration (Stockmarr, 1971) before preparation that followed standard procedures, including KOH, HCl, HF, and acetolysis (Fægri and Iversen, 1989). The residues were mounted in silicone oil. An average of 500 terrestrial pollen grains was counted per sample, plus spores, algae, and other palynomorphs. All terrestrial pollen

**Table 1**
Results of AMS radiocarbon dating performed on terrestrial remains from the Slotseng series. The column labeled A gives the agreement index used for rejection of dates not used in the model.

| Lab code | Material | Depth (m a.s.l.) | $\delta^{13}C$ (‰ VPDB) | $^{14}C$ age (yr BP) | Model age (cal yr BP) | A |
|---|---|---|---|---|---|---|
| Ua-19217 | Twigs | 34.47 | −17.7 | 14180 ± 165 | 16673 ± 280 | 83% |
| Ua-19218 | Twigs | 34.49 | −28.8 | 12730 ± 265 | 15540 ± 348 | 64% |
| Ua-19886 | Twigs | 34.55 | −28.0 | 13270 ± 125 | 14728 ± 255 | Outlier |
| Ua-19887 | Twigs | 34.56 | −22.5 | 12620 ± 200 | 14593 ± 239 | 105% |
| Ua-19219 | Twigs | 34.59 | −28.6 | 12640 ± 190 | 14232 ± 81 | 54% |
| Ua-19888 | Twigs | 34.60 | −25.6 | 12265 ± 120 | 14225 ± 78 | 123% |
| AAR-9822 | Leaf fragment of *Betula nana* and *Dryas octopetala*, twig unknown | 34.60 | −26.51 | 12490 ± 140 | 14225 ± 78 | 81% |
| Ua-19220 | Twigs | 34.67 | −27.8 | 12365 ± 110 | 14178 ± 60 | 117% |
| Ua-19889 | Twigs | 34.69 | −29.0 | 11965 ± 120 | 14164 ± 56 | Outlier |
| Ua-19890 | Twigs | 34.73 | −28.9 | 12175 ± 120 | 14137 ± 48 | 110% |
| AAR-9823 | 1 fruit, and 16 catkin scale of *B. nana*. Leaf fragment of *D. octopetala* | 34.73 | −26.16 | 12460 ± 75 | 14137 ± 48 | Outlier |
| Ua-19222 | Twigs | 34.76 | −28.0 | 12425 ± 115 | 14118 ± 44 | Outlier |
| Ua-19891 | Twigs | 34.77 | −26.8 | 12200 ± 135 | 14111 ± 43 | 147% |
| Ua-19892 | Twigs | 34.78 | −27.7 | 12035 ± 130 | 14105 ± 43 | 45% |
| Ua-19893 | Twigs | 34.84 | −27.6 | 12185 ± 130 | 14070 ± 42 | 151% |
| Ua-19894 | Twigs | 34.85 | −28.4 | 12390 ± 160 | 14064 ± 42 | 69% |
| Ua-19895 | Twigs | 34.86 | −28.2 | 12280 ± 125 | 14058 ± 43 | 132% |
| AAR-9850 | 8 fruit, and 12 catkin scale of *B. nana*. 6 twigs possibly *B. nana*. Leaf fragment of *D. octopetala* | 34.92 | −27.62 | 11830 ± 70 | 14020 ± 52 | Outlier |
| Ua-19896 | Twigs | 34.99 | −27.8 | 12145 ± 120 | 13976 ± 62 | 133% |
| Ua-19897 | Twigs | 35.00 | −27.0 | 12125 ± 135 | 13970 ± 64 | 137% |
| Ua-19898 | Twigs | 35.01 | −27.4 | 12115 ± 120 | 13963 ± 66 | 129% |
| AAR-9824 | 8 twigs – terrestrial | 35.20 | −27.21 | 11890 ± 70 | 13752 ± 54 | 117% |
| AAR-9825 | 7 twigs – terrestrial. 2 *B. nana* fruit | 35.35 | −26.72 | 11680 ± 80 | 13550 ± 77 | 109% |
| AAR-9826 | 2,5 $cm^2$ *Betula pubescens/nana* leaf fragment | 35.48 | −29.44 | 11305 ± 75 | 13251 ± 51 | 82% |
| AAR-9827 | 3,0 $cm^2$ *B. pubescens* leaf fragment | 35.52 | −26.76 | 11400 ± 75 | 13185 ± 45 | 70% |
| AAR-9882 | Twig *B. pubescence* | 35.60 | −27.57 | 11120 ± 60 | 13000 ± 51 | 103% |
| AAR-9830 | 1,0 $cm^2$ *B. nana* leaf fragment. 8 *Betula nana* fruit | 35.74 | −28.18 | 10390 ± 65 | 12520 ± 102 | 57% |
| AAR-9831 | 3 *B. nana* fruit and *B. nana* leaf fragment. 4 twigs. | 36.05 | −26.94 | 10635 ± 70 | 11675 ± 179 | Outlier |
| AAR-9832 | 1 *B. nana* fruit and 1 *Betula* bud scale. | 36.19 | −28.00 | 9960 ± 90 | 11392 ± 87 | 120% |
| AAR-9849 | 2 twigs probably *B. pubescence* | 36.25 | −27.41 | 9935 ± 60 | 11281 ± 44 | 116% |
| AAR-9833 | 1 twigs probably *B. pubescence* | 36.31 | −27.71 | 9600 ± 70 | 11143 ± 47 | 68% |
| AAR-9834 | 5 twigs probably *B. pubescence* | 36.42 | −29.15 | 9650 ± 60 | 10954 ± 106 | 96% |

and spores were included in the pollen sum. *Sphagnum* and Cyperaceae were excluded because of their overwhelming local abundance. Whole slides were analyzed to avoid effects of unequal distribution of pollen under the cover slip. Beug (2004) was consulted for general pollen identification, supplemented by the reference collection at the National Museum of Denmark for problematic grains and specialist works for the following: Punt and Blackmore (1991); Punt et al. (1995) for *Cerastium cerastoides* g., *Cerastium fontanum* g., *Thalictrum alpinum* g., *Thalictrum flavum* g., Moore et al. (1991) for *Oxyria*, *Equisetum*, Fægri and Iversen (1989) and Moe (1974) for spores, and van Geel (1976) for non-pollen palynomorphs. Although the grain size of *Betula nana* tends to be smaller than that of tree birches, an absolute separation is impossible since their size distributions overlap (e.g. Birks, 1968; Usinger, 1977; Andersen, 1980). Therefore a fixed threshold at 21.5 μm was used for dividing a *B. nana* type from a tree birch type (e.g. Kolstrup, 1982; Karlsdóttir et al. 2007). These measurements supplement the macrofossil analysis, which is a more powerful way of differentiating *Betula* species. Many *Betula* grains in the upper eight samples showed signs of exine damage and were not measured. Judged from size and morphology, they were recorded as tree birch type. Pollen of thermophilous taxa such as *Alnus*, *Carya*, *Corylus*, *Ilex aquifolium*, *Juglans regia*, *Picea*, *Platycarya*, *Pteridium aquilinum*, *Quercus*, *Tilia*, *Taxus*, *Ulmus* and *Viscum album* were regarded as rebedded if present in the late-glacial deposits. *Carya* and *Platycarya* are most likely redeposited from nearby Miocene brown coals while the rest probably derive from various interglacial deposits. Charred fragments >10 μm were counted. The pollen (Figs. 4 and 5) and macrofossil (Fig. 6) data were plotted using Tilia (2.0.2. Grimm, 2000), TGView (2.0.2. Grimm, 2004) and C2 (1.6.1. Juggins, 2009). Plant nomenclature follows Wisskirchen and Haeupler (1998).

### 3.4. Macrofossil analysis

Of the 66 levels analyzed for pollen 47 were also analyzed for macrofossils. Sediment volume (mean of 70 $cm^3$) of the 1 cm thick samples was measured by displacement of water and samples were wet sieved through a 125 μm mesh. When necessary, sodium pyrophosphate was added to soften the sediment before sieving. Macrofossils were identified and counted at 10–40× magnification. The reference collection at the Department of Biology, University of Bergen, was consulted for identification together with identification guides (Beyerinck, 1976; Nilsson and Hjelmqvist, 1976; Aalto, 1970). The cell-pattern and morphology was used to determine leaf fragments of *Betula* to species level (Wagner et al. 2000). Frequency of taxa represented by high numbers of fossils was estimated from quantitative subsamples. The abundances of remains that cannot be counted, including leaf material of *Betula* and *Dryas*, mosses, twigs, and Characeae oospores, were estimated and given the following scores in the further calculations: present (2), rare (4), occasional (10), frequent (25), abundant (100), very abundant (200). Other fossils are presented as numbers per 100 $cm^3$ fresh sediment in Fig. 6.

### 3.5. Numerical analyses

Based on pollen percentage and macrofossil concentration data local assemblage zones were delimited by optimal splitting using

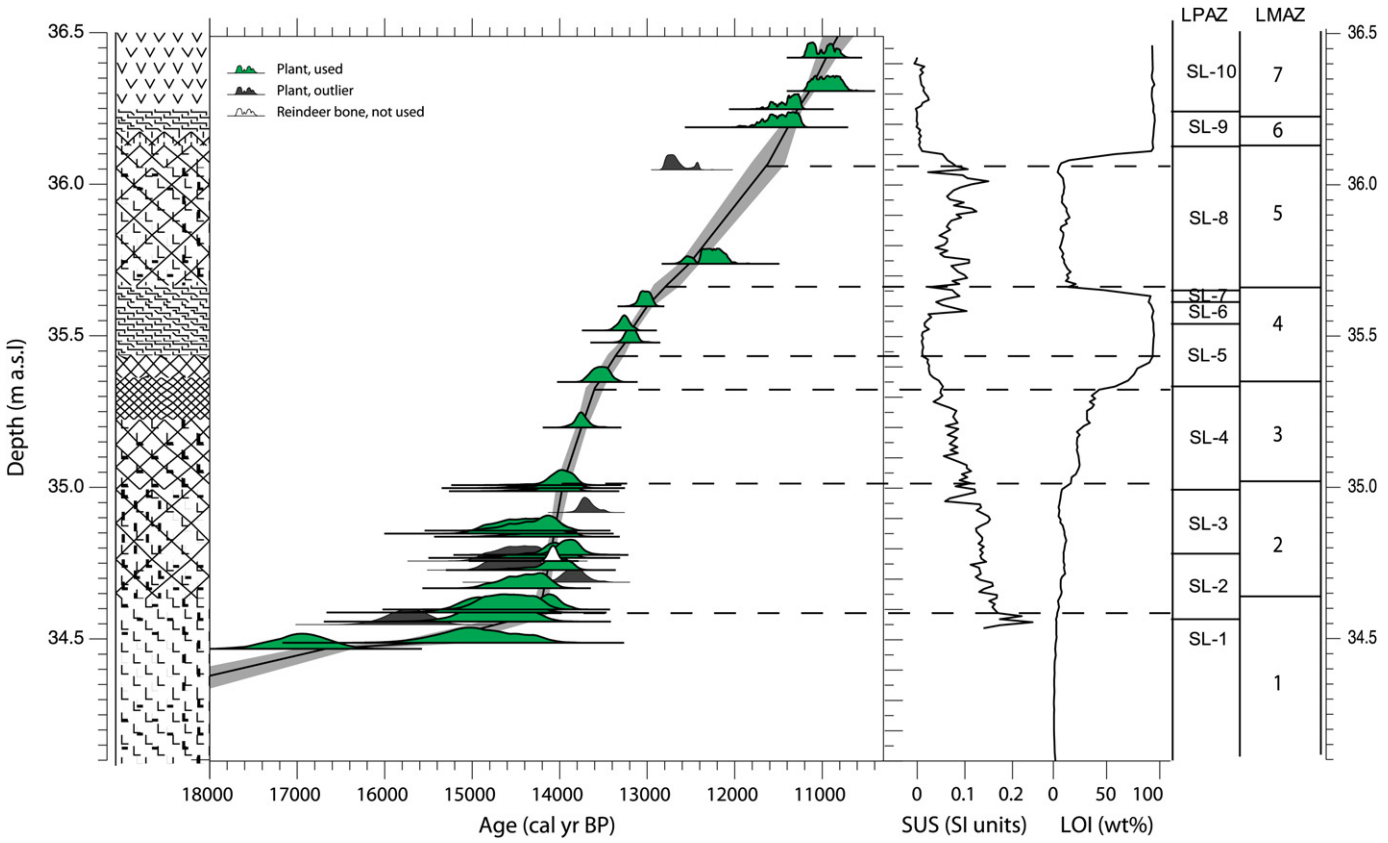


**Fig. 3.** Bayesian age-depth model for the Slotseng stratigraphy together with profiles of lithostragiraphy, sediment accumulation rate. The dashed lines indicate lithological changes used to add boundaries into the constructed age model. Lithostratigraphic symbols are keyed on Fig. 4. Local pollen and macrofossil assemblage zones are shown in the left hand side.

information content as a dissimilarity coefficient implemented in psimpoll 4.10 (Bennett, 2002). Aquatic plants were excluded. To avoid bias from rare taxa and taxa with low frequency, only taxa present in more than 5% of the samples and with a frequency >1% for pollen and >5% for macrofossils (converted to percentages for this analysis) were included. A broken-stick model (Legendre and Legendre, 1998) as implemented in psimpoll 4.10 was used to determine the numbers of "significant" zones. Since the zonation of the pollen data was affected by the marked changes at the Younger Dryas–Holocene transition, zonation was performed on the late glacial and the Holocene samples separately. This distinct boundary was subsequently reinstated.

To aid the interpretation of late-glacial pollen assemblages the pollen analytical results are presented as percentage and accumulation rate data (Figs. 4 and 5). Based on the taxa included in the terrestrial pollen sum, palynological rate-of-change and evenness were calculated (Fig. 7). Rate-of-change is a quantitative estimate of change per unit time (Bennett and Humphry, 1995). Chord distance was used as a measure of dissimilarity and samples were selected at intervals of approximately 100 years. Intermediate samples were deleted. Evenness is a measure of the distribution of individual taxa as pollen types. By inference, palynological evenness may be related to vegetational evenness and thus to the interspecific competition (Odgaard, 2001). Low vegetational evenness indicates high interspecific competition, while high evenness indicates low interspecific competition (Legendre and Legendre, 1998). Since competition is partly controlled by disturbance, evenness may also relate to the level of disturbance in the catchment area (Odgaard, 2001). The Shannon diversity index divided by its maximum value was used as a measure of evenness:

$$\frac{\left(-\sum_{i=1}^{q} p_i \log p_i\right)}{\log q}$$

where $p_i$ is the proportion of pollen type $i$, and $q$ is the number of taxa in the sample.

Ellenberg ecological indicator values (primarily Ellenberg et al. 1992 with supplemnts from Hill et al. 2000) for soil nitrogen (N), soil reaction (R), and light (L) were ascribed to each terrestrial macrofossil taxon in an attempt to quantify changes in soil development. Only taxa with Ellenberg values 1–7 for moisture (F) - habitats from extreme dryness to moist soil - were selected. Based on the Ellenberg scores on presence/absence data an average was calculated for each sample and used as an index value. Ellenberg indicator values are expressions of realized plant species niches in relation to one-dimensional resource availabilities (Ellenberg et al., 1992). Soil nitrogen (N) originally designated the amount of nitrogen available during the growing season. However, a number of studies has shown that this index correlates strongly with plant biomass (Hill and Carey, 1997; Schaffers and Sýkora, 2000; Wagner et al., 2007). 'R' is strongly correlated to soil calcium content (Schaffers and Sýkora, 2000). Realized plant niches and hence Ellenberg values show geographical variation and may not have been stable over time. However, we use them here as a rough indication of the direction of changes in resource availability.

To explore the temporal patterns of the species changes, detrended correspondence analysis (DCA, Hill and Gauch, 1980) was applied to the pollen percentage and macrofossil data. For the macrofossils, their frequency was standardized against the maximum abundance of each fossil taxon (Odgaard and

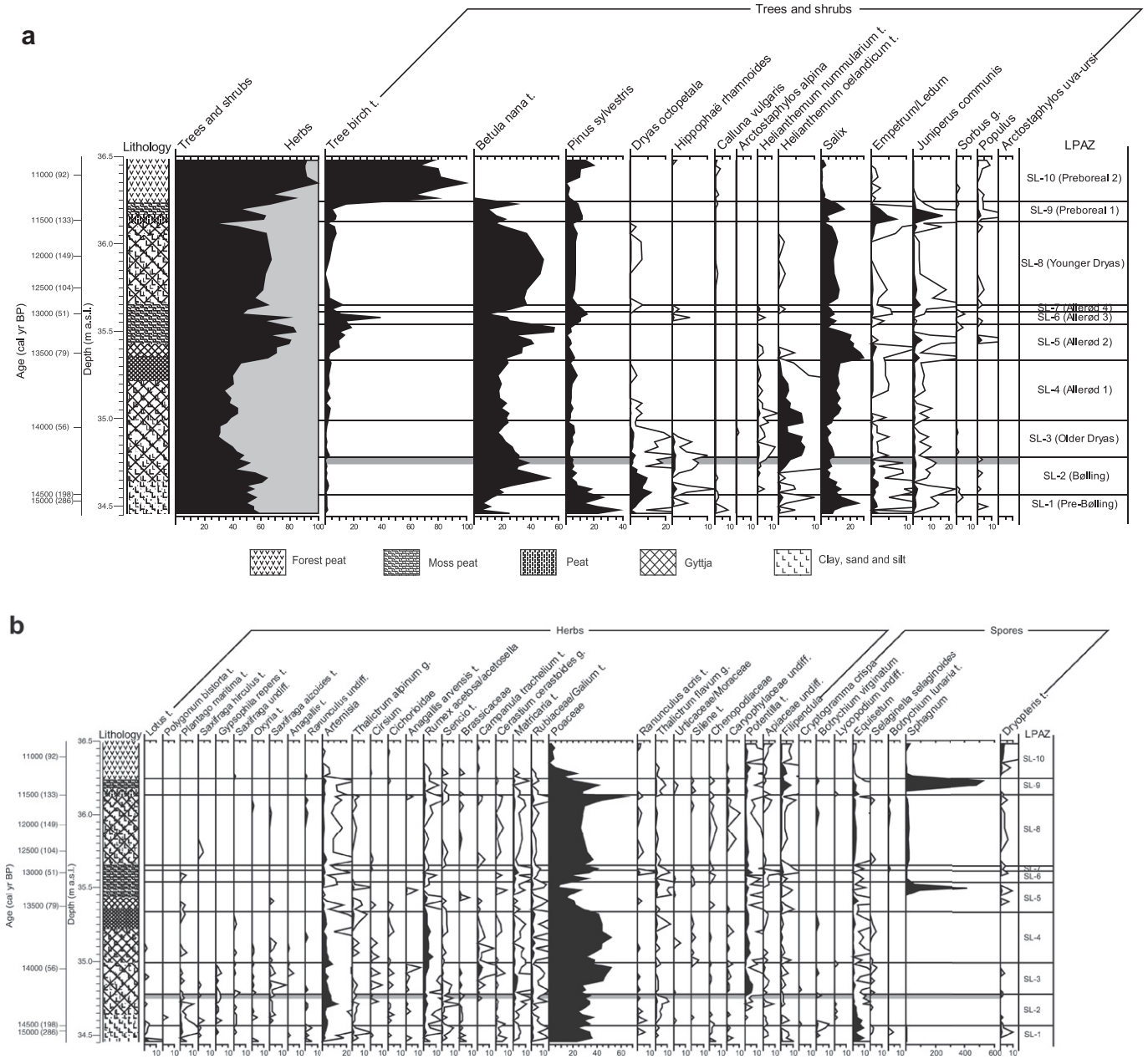


**Fig. 4.** Pollen percentages diagram showing selected taxa. The sum used for percentage calculations is terrestrial pollen and spores except *Sphagnum* and *Cyperaceae*. The open outline is an ×10 exaggeration of the percentage values. The grey horizontal line indicates the depth (34.74–34.78 m a.s.l.) of Paleolithic flint implements, reindeer bones and antlers. g. = pollen group, t. = pollen type.

Rasmussen, 2001) in order to down-weight the bias by strongly dominant taxa inherent in macrofossil assemblages (Birks and Birks, 1980). Concentrations of fossils in all samples were thus transformed into a 4-level frequency scale according to the following scheme:

Abundant: $x \geq m$, Common: $n < x \leq m$, Rare: $0 < x \leq n$, Absent: $x = 0$.

where $x$ is the square root concentrations of a plant remain in a sample (no. in 100 $cm^3$ fresh sediment), $m$ is the mean square root concentration of fossils of this type in all samples containing this type, and n is the mean square root concentration of this type in all 47 samples.

DCA was performed using CANOCO 4.5 (Ter Braak and Smilauer, 2002) with detrending by segments, downweighting of rare taxa, and all other settings default. The gradient length of 2.231 for axis 1 of the pollen data suggests that species responses to environmental gradients can be modeled using linear models (Leps and Smilauer, 2003). Samples in a stratigraphic sequence are a time series with temporal autocorrelation between samples (Ter Braak and Smilauer, 2002). To try to minimize at least linear autocorrelation, sediment age was used as a covariable (Odgaard, 1994).

Lateglacial pollen records are frequently interpreted only in the context of climate change (e.g. Lotter et al., 2000; Bordon et al. 2009), However, forcing mechanisms of vegetational changes may shift over time between e.g. climate change, soil erosion, or soil development. In an attempt to identify the most important factors determining the pollen record at Slotseng, RDA was applied to subsets of pollen data representing a moving window (Bradshaw

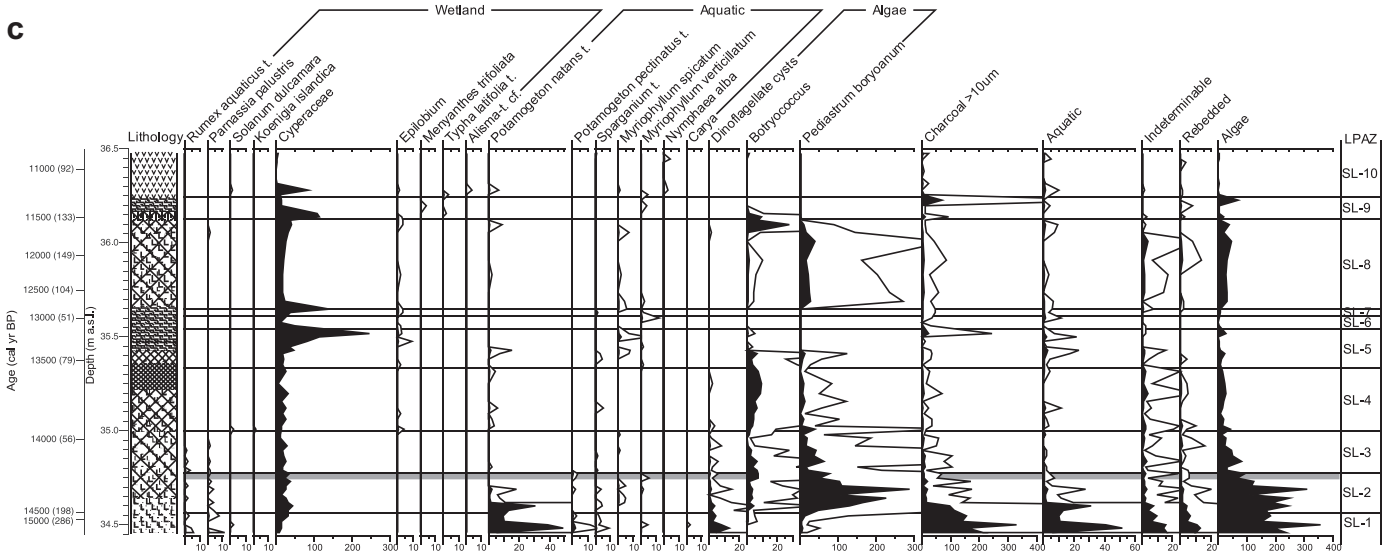


**Fig. 4.** (*continued*).

et al. 2005) of 20 samples at a time (samples 1–20, 2–21, 3–22, etc.). Sediment age was used as a covariable and explanatory variables representing environmental change were soil nitrogen, R, and light (all inferred from the Ellenberg indices estimated from macrofossil results), LOI, SUS, sediment accumulation rate, presence of tree-birch macrofossils, sediment type (peat/gyttja), and $\delta^{18}O$ from assumedly synchronous levels in the NGRIP and GRIP ice cores. These $\delta^{18}O$-values were used here as a general proxy of rate of climate variability rather than directly as a temperature proxy. Downweighting of rare species was applied and permutations were restricted for time series. Manual Bonferroni-adjusted forward selection was used to identify significant explanatory variables (Monte Carlo permutation tests, $n = 999$). With these settings the permutation tests were run for the 47 macrofossil samples for which all data types were available under the reduced model (Ter Braak and Smilauer, 2002).

## 4. Results

### 4.1. Age-depth model

The chronology of the Slotseng basin is based on 32 $^{14}C$ dated samples of plant macrofossils (Table 1, Fig. 3). Below 35 m a.s.l. the dates show large scatters in their calibrated ages and six outliers are detected using the agreement index A and the general outlier model of OxCal 4.1 (Ramsey, 2009). The remaining 26 $^{14}C$ samples were used to construct the age model employing the depositional model option in OxCal 4.1 with a model parameter $k = 100$ (Ramsey, 2008). The observed lithological changes, SUS, and LOI values were used to add boundaries into the constructed age model allowing for changes in sedimentation rates at these depths (Fig. 3). The resulting age model yielded a model agreement index of 72.1%. The uncertainties on the ages range between 50 and 170 years

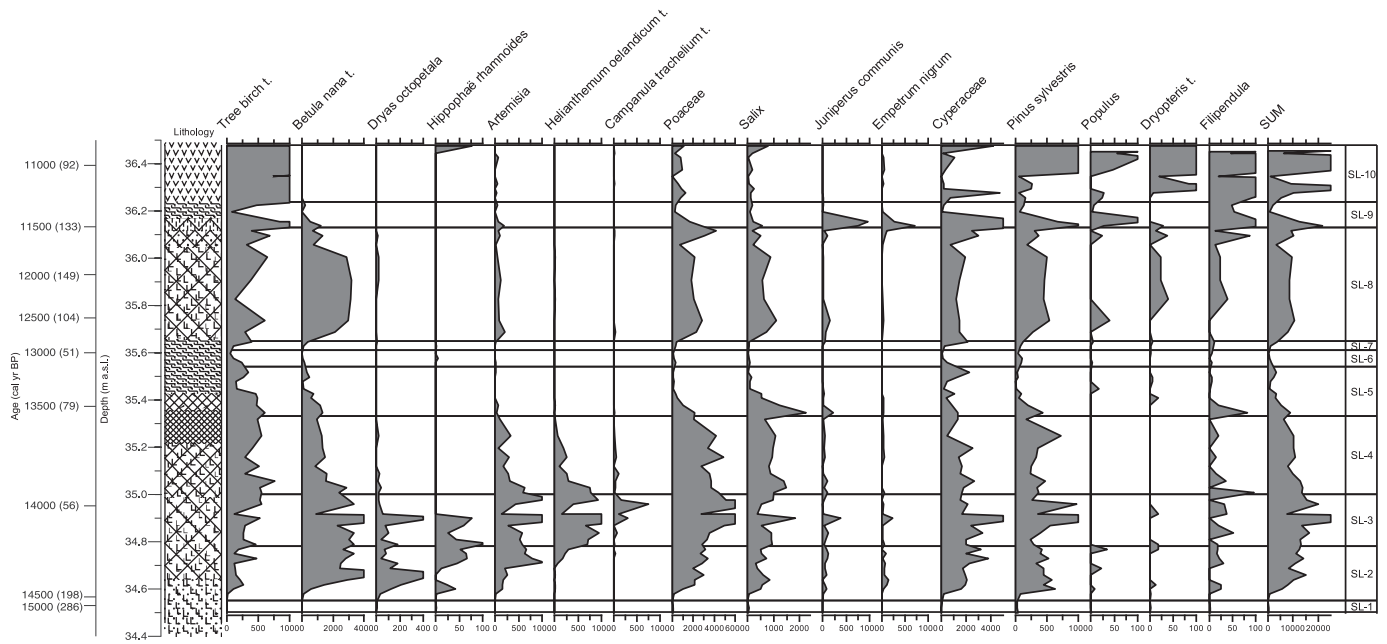


**Fig. 5.** Pollen accumulation rate (grains $cm^{-2}$ $y^{-1}$) diagram showing selected taxa. Note changes in *x* axis scales.

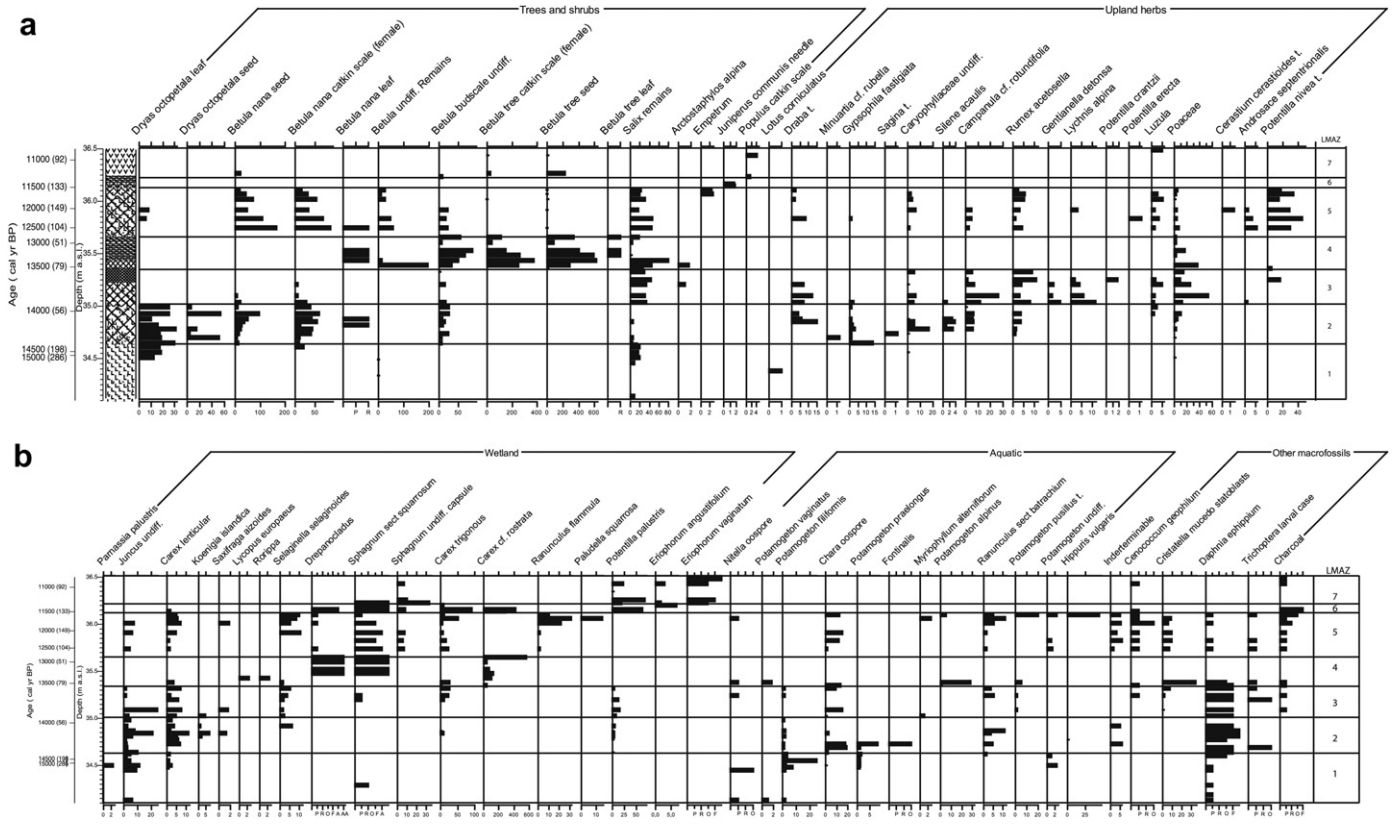


**Fig. 6.** Diagram showing macrofossil concentrations in 100 ml sediment. The taxa are seeds or fruits, unless otherwise indicated. t = macrofossil type.

except for depths lower than 34.59 m a.s.l where extrapolated ages are associated with uncertainties of up to 1200 years towards the bottom of the section.

Four of the six $^{14}$C sample outliers were older than expected and probably reflect reworked older material (Fig. 3). The remaining two outliers appeared too young (Fig. 3). The calibrated age probability distribution of sample Ua-19889 (34.69 m a.s.l.) overlapped peripherally with the age model whereas AAR-9850 (34.92 m a.s.l.) was considerably younger (Fig. 3). We cannot explain these young ages and note that they cannot be included in the age model without compromising all the $^{14}$C samples between 35.0 and 35.5 m a.s.l. (Fig. 3). The $^{14}$C dates measured on ten reindeer bones yielded a combined mean age of 12,222 ± 29 $^{14}$C yrs BP (14,180–13,980 cal yr BP). The calibrated age probability distribution of the combined $^{14}$C reindeer is in excellent agreement with the constructed age model giving further support to the

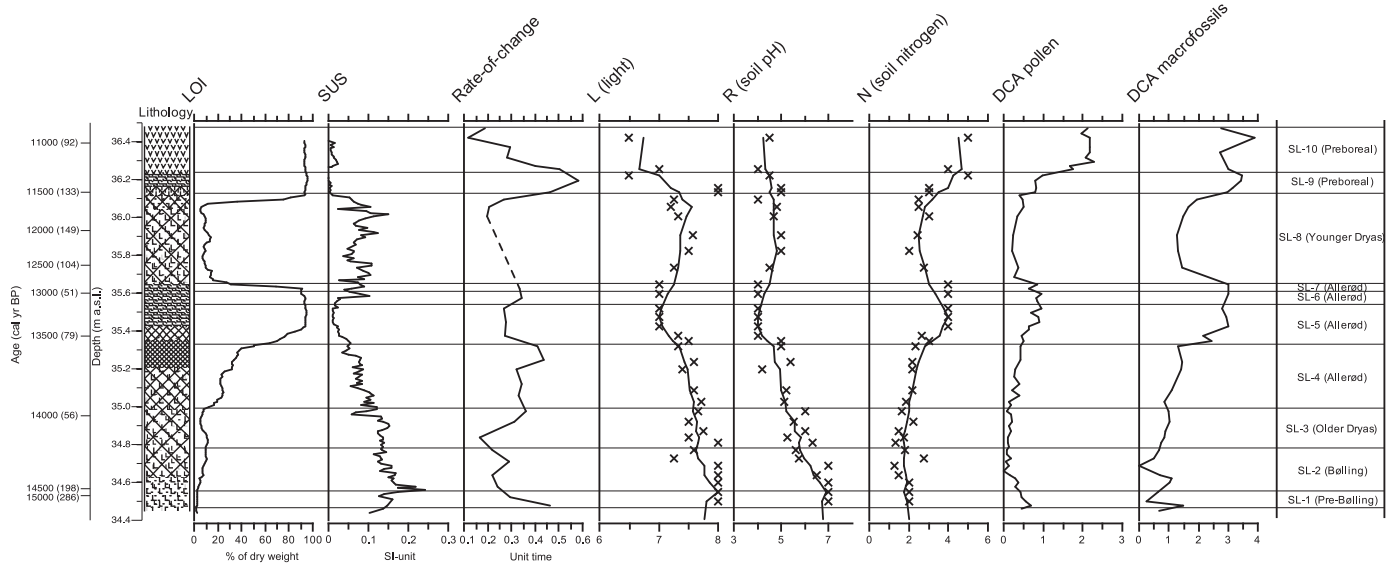


**Fig. 7.** Loss on ignition (LOI), magnetic susceptibility (SUS) and palynological rate-of-change in the Slotseng series. Macrofossil-inferred light (L), soil reaction (R), and nitrogen (N) are based on Ellenberg indices (Ellenberg et al., 1992; Hill et al., 2000). The line in the macrofossil inferred light, pH and nitrogen shows a running mean of 5. DCA sample scores on 1 axis are based on pollen and macrofossil data.

interpretation that the dating results of the samples Ua-19889 and AAR-9850 are unreliable (Fig. 3). Sharp sedimentary changes at 35.66 m a.s.l. may suggest the occurrence of a hiatus. Because of the few radiocarbon dates in the Younger Dryas period we have been unable to estimate the length of any such hiatus and the age/depth model has been made continuous across this level (Fig. 3).

### 4.2. Stratigraphy

The stratigraphy of the monoliths was divided into 12 lithological units based mainly on the Troels-Smith (1955) sediment descriptions (Supplementary data Table 2). The sediment structure varies highly in time (vertically) between lacustrine deposits and peat, as well as in space (horizontally). However, the majority of the strata can be followed across the basin (Fig. 2). LOI and SUS of each unit are presented in Fig. 7.

The sediment lithology is a reflection of the hydroseral development of the Slotseng basin. It started as a small lake after the ice sheet had retreated. In the first phase of the basin development there are indications that dead ice was still entombed beneath the lake floor. During the Bølling and Older Dryas period the dead ice gradually melted and water depth increased accordingly. This development along with the influence of different disturbances such as slumping, erosion, and ice rafting of sediment has created a variable stratigraphy. The availability of an open section was an enormous advantage in detecting this variability, which could be highly puzzling if only a single core was available. During the Allerød period a telmatic stage was reached when a mat of *Drepanocladus* and *Sphagnum* covered the basin. In the Younger Dryas a new limnic stage was initiated. Then the lake basin gradually filled and was transformed into a fen that was subsequently overgrown by forest during the early Holocene. Further details about the lake development based on the sedimentary studies are given by Mortensen (2007).

### 4.3. Local assemblage zones

The numerical zonation of the pollen record resulted in nine "significant" zones. Two modifications to the numerical zonation were made: The division between SL-1 and SL-2 estimated by optimal splitting at 34.61 m a.s.l. where *B. nana* increased rapidly, was moved to 34.55 m a.s.l. where the first increase in *Pediastrum boryanum* is recorded (it was not used in the zonation data). This is because these shifts are most likely representing the first limnological and vegetational responses to a warming. The second modification is the addition of an extra boundary at the shift between peat and lacustrine sediment at 35.65 m a.s.l. which marks the Allerød – Younger Dryas transition. The general development in the pollen record is described in Supplementary data Table 3 and the percentage and accumulation rate pollen diagrams are shown in Figs. 4 and 5.

The numerical zonation of the plant macrofossil record resulted in seven "significant" zones (LMAZ) at Slotseng. Each plant macrofossil zone is described in Supplementary data Table 4 and the macrofossil diagram is shown in Fig. 6.

### 4.4. Evenness and rate-of-change

Pollen evenness shows relatively constant values around 0.6 from SL-1 to SL-9. The only major change in evenness is recorded at the transition from SL-9 to SL-10 where the values are reduced to approximately 0.3. The rate-of-change was relatively constant from SL 1 to SL 7 with a local minimum in SL 5 followed by a peak of change in SL 6. Due to an assumed minor hiatus between zone SL-7 and SL-8 there is a gap between the samples at this level. In SL-9 the rate-of-change increased rapidly and then decreased after the transition to SL-10.

### 4.5. Ellenberg indices

Macrofossil taxa and associated Ellenberg values used for estimating changes in the environmental conditions are listed in Supplementary data Table 5. Changes in the indices through time are shown in Fig. 7. The inferred light index shows a general tendency towards lower values through the sequence, with minima from SL-5 to SL-7 and from SL-9 to SL-10. The light index generally decreases through to the end of the Allerød. It increases again during the Younger Dryas but decreases considerably with the development of woodland in the early Holocene. The inferred Ellenberg soil R decreases from 7 (weakly basic soil) in SL-1 and SL-2 (Bølling) to 4 (between neutral and mainly acid soil) during SL-6 and SL-7 (late Allerød). The R value increases slightly again in the Younger Dryas and the early Holocene, after SL-7 (Fig. 7). The inferred Ellenberg soil nitrogen shows low values around 2 (between extremely infertile soil and more-or-less infertile soil) at the beginning of the sequence and increases in SL-5 and SL-6 to an index value of 4 (low-intermediate fertility) (Fig. 7). During SL-8 (Younger Dryas) the values are reduced to approximately 2.5. In SL-9 the values rise again to 5 (intermediate fertile soil).

### 4.6. Detrended correspondence analysis

The first axes of the DCAs explain 44.9% and 11.3% of the total inertia in the pollen and the macrofossil data, respectively (Fig. 7). Pollen taxa with low scores on axis 1 are especially light-demanding species such as *Astragalus alpinus*, *Helianthemum*, *Rumex acetosella*, *Dryas*, and *Hippophaë*, while pollen taxa with high positive scores are mostly shade tolerant and shade giving species such as tree birch, *Populus*, and *Dryopteris* (Supplementary data Table 6). Pollen axis 1 can thus be interpreted as a shade-light gradient from open landscapes towards birch forest. Macrofossil taxa on DCA axis 1 likewise reflect a shade-light gradient with light-demanding species such as *Silene acaulis* and *Koenigia islandica* with lowest scores, and more shade tolerant species such as *Populus*, *Eriophorum vaginatum*, *Juniperus communis*, and *Lycopus europaeus* with the highest positive scores. The first axes were plotted stratigraphically (Fig. 7) and they summarise the overall directions of variation through the sequence.

### 4.7. Environmental forcing

Based on the sequential RDAs (Supplementary data Fig. 8) four overall, but overlapping regimes forcing palynological change can be identified.

1. From pre-Bølling to early Allerød GRIP and NGRIP ice-core $\delta^{18}O$ (proxy for climate change), soil nitrogen, SUS, and LOI explain between 37.7% and 27.7% of the variation in the pollen data.
2. When excluding the early part of the Bølling, the variation in the pollen data until the end of Allerød is dominated by forcing related to changes in sediment type (LOI, peat) and climate (NGRIP $\delta^{18}O$). These factors together explain between 42.2% and 16.0% of the variation in pollen assemblages.
3. The changes in pollen assemblages between the beginning of the Allerød and the end of Younger Dryas are most strongly related to variations in light, SUS, sediment type (peat), and soil R. These factors together explain between 54.8% and 39.2% of the variation.
4. The pollen changes during the period from the mid Allerød to the end of the Preboreal are most strongly related to the presence/absence of tree birch macrofossils and variations in

LOI and inferred soil nitrogen. These factors together explain between 57.7% and 18.3% of the variation.

## 5. Discussion and environmental synthesis

### 5.1. Factors affecting vegetational responses at Slotseng

Climate is an obvious driving factor during the Lateglacial. However, climatic changes are mediated by local factors and biotic thresholds. On land these include migration into a recently deglaciated landscape, soil development, including its base status (R) and nutrient (N) content, and light availability. In the lake, factors include water depth, water chemistry and base-status, productivity, presence of macrophytes, and inwash of minerogenic and organic material from the catchment (Birks et al., 2000; Birks and Birks, 2006).

Our proxies of soil development during the late glacial and early Holocene are mean Ellenberg values (Ellenberg et al. 1992; Hill et al. 2000) of N and R estimated from the plant macrofossil assemblages. These are minimal estimates, because not all the macrofossil taxa have published indices (e.g. *Gentianella detonsa*) while for others the taxonomic resolution is too low to ascribe a representative index value. It could be argued that the use of a simple average of the index could be refined by using an average weighted by frequency. However, due to the great range in the representation of macrofossil remains (Birks, 2001) such a procedure is not straightforward. The mean index values shown in Fig. 7 reflect a consistent and plausible development from a basic soil during the early late glacial to a gradually more acid state. Similarly, inferred soil N (proxy of productivity), as expected, gradually increased as soils developed through the late glacial only interrupted by the Younger Dryas cooling. These trends indicate improved conditions for plant growth which are clearly reflected in the increased competition for light during the period as reflected by both the pollen and macrofossil DCA axis 1 scores (Fig. 7) as well as by the Ellenberg light index (Fig. 7), again interrupted by the Younger Dryas set-back. Pollen sample evenness (not shown) was more or less constant until it decreased in the early Holocene when competitive exclusions became significant (mainly from tree-birch development).

The late-glacial climate variations, recorded in numerous biological, physical, and chemical proxies all over the North Atlantic region (e.g. Walker, 1995; Björck et al., 1996), would be expected to be the overall factor driving the vegetational responses in Denmark. However, our series of RDA's (Fig. 8) show that climate variations as expressed by the proxy ice-core $\delta^{18}O$ had little significant correlation with our pollen data. Provided chronologies of the two sedimentary systems are in reasonable agreement, the low explanatory power of climatic change could be caused by strong catchment–lake interactions which mask or decouple the biotic responses to climate changes. In addition, the low explanatory power may be due to the time lag that inevitably exists between climatic change as recorded in ice cores and the responses of many parts of biological systems. Such delayed responses during the late glacial would be related to unstable and immature soils as well as to migrational lags. Refugia of most temperate species were in Central and southern Europe and northwards expansions were not instantaneous (Huntley and Birks, 1983; Willis and van Andel 2004; Svenning and Skov, 2005, 2007). Also, the confounding effect of long-distance transported pollen tends to make palynological changes slower.

Until the early Allerød the vegetation was dominated by pioneer communities the changes in which were related to variation in LOI, soil nitrogen, and temperature, which was undoubtedly driving the other ecosystem factors indirectly (Fig. 8). Low soil nitrogen content is like to have been an important limiting factor for the early vegetational development. Later, until the end of Allerød period, LOI was the dominant explanatory variable for the variations in pollen data. LOI is a reflection of the proportions of organic and minerogenic material, both of which can be derived from the catchment and the lake (Birks and Birks, 2006). The early link between LOI and vegetation response may well be an initially sparse vegetation cover with low productivity and relatively high disturbance rates leading to minerogenic input. However, the high explanatory power of LOI continues, related to the reflection of the local hydrological development within the lake by the pollen assemblages as the hydrosere proceeded from lacustrine towards telmatic conditions in the early Allerød. This would affect pollen dispersal into and within the basin and minerogenic input would be reduced. During the Allerød, a moss-dominated community covered the basin forming almost totally organic peat, and the upland pioneer vegetation was replaced by a denser vegetation of more competitive species. At the start of the Younger Dryas, a dramatic return to lacustrine conditions and more open vegetation occurred associated with catchment soil erosion, decreased N, and low LOI, followed in the early Holocene by a rapid increase in organic content associated with climate warming and hydroseral and soil development. LOI is a very good summarising variable for local basin and vegetation dynamics, as shown by its high degree of correlation with the pollen data (Fig. 8). It is also related to SUS, which is usually higher in more minerogenic sediment (Fig. 7). SUS closely parallels LOI over the Allerød-Younger Dryas transition. This link between vegetation response and these environmental factors is probably related to the disruption of the vegetation cover at the transition to the Younger Dryas and the associated stronger soil erosion. For the transition Allerød/Younger Dryas/Preboreal local soil and vegetation development is well explained by soil N and LOI. In the Preboreal, the presence of *Betula* tree macrofossils has high explanatory power for the pollen assemblages suggesting competition for light as a dominant driving factor for vegetation.

The series of canonical ordinations highlight the multitude of climatic, physical, chemical and biological interactions important for the formation of pollen records of late glacial vegetation changes. This result strongly suggests that late glacial pollen records should not be interpreted merely as a direct climate proxy.

### 5.2. Vegetation history

The local pollen assemblage zones are used as a frame for the following discussion in order to facilitate the interpretation of the vegetation development at Slotseng. These zones correlate with the regional vegetation development and the terminology follows the traditional Danish stratigraphy (Iversen, 1954; Andersen, 1980) (Supplementary data Table 7).

#### 5.2.1. Pre-Bølling: (SL-1) pre-Bølling to 14,700 cal yr BP

Due to lack of $^{14}C$ dates in bottom part of the sequence the timing of the onset of the sedimentation in the basin is unknown. Extrapolation of the age model towards the bottom depth of 34.1 m a.s.l provides an age estimate of 22,200 ± 1160 cal BP. This result, is considerably older than the suggested deglaciation of the area around c. 19,000 cal BP (Houmark-Nielsen and Kjær, 2003) and it is likely that the oldest radiocarbon date at 34.48 m a.s.l. overestimates the age of the deposit or that sedimentation rate was not constant below this level. Being a kettle hole it is unlikely that sedimentation took place in the basin immediately after deglaciation but we are not able to determine the exact age of the onset of sedimentation. During the pre-Bølling phase the landscape was sparsely vegetated and strongly influenced by periglacial condition such as permafrost, erosion, aeolian activity, and

solifluction. Soils were poor in nitrogen and humus, but unleached and relatively basic (Fig. 7). Unstable environmental conditions favoured stress-tolerant pioneer vegetation that benefited from an assumed high concentration of phosphorus and other minerals in the raw soil (Born and Böcher, 1999). Stratigraphical evidence (Mortensen, 2007) indicates that at this stage the lake was shallow due to the basin floor being elevated by the presence of buried dead ice.

Evidence for vegetational development is taken from the pollen record (Figs. 4 and 5) and the macrofossil record (Fig. 6). A relatively diverse aquatic flora was already present in the lake including *Potamogeton filiformis*, *P. vaginatus*, *P. praelongus*, *Nitella* sp., *Chara* sp., *Myriophyllum verticillatum*, and *Myriophyllum alternifolium*. These taxa all have wide ecological amplitudes and are characteristic of clear water with high conductivity and conditions of low inter- and intraspecific competition. *Juncus* sp. grew in moist soil by the lake. However, the pollen assemblage includes many thermophilous taxa and is therefore most likely biased by rebedded material. The reconstruction of the pre-Bølling terrestrial vegetation is therefore somewhat uncertain.

Pollen influx was extremely low in zone SL-1 and macrofossils were sparse, suggesting that terrestrial vegetation was in the earliest stages of colonisation of the deglaciated landscape. The pollen assemblage contains some assumedly primary arctic-alpine taxa that readily colonise open ground, such as *Oxyria digyna*, *Cerastium cerastoides*, *Rumex acetosella* type, Brassicaceae, and *Thalictrum alpinum*, but arctic-alpines are not a prominent component of the flora. Other pioneer types represent thermophilous steppe and weed elements, including *Helianthemum oelandicum* type, *Lotus* type, *Plantago media/major*, *Plantago maritima*, *Gypsophila repens*, *Matricaria* type, and Rubiaceae/*Galium*. None of these pollen types is represented by macrofossils, suggesting that although they could have been locally present, their pollen may also have been blown in from the extensive arctic steppe and plains further south and east (see Iversen, 1973). Macrofossils and pollen of *Salix* are present, probably from the dwarf species *Salix polaris* or *S. herbacea*. These species were among the first vascular plants to colonize former glaciated areas in Denmark (Bennike and Jensen, 1995; Jensen et al. 1997; Bennike et al. 2004b) and southern Sweden (Jönsson, 1988). With its capability to grow on unstable raw soil and to withstand low summer temperatures *S. polaris* was an important pioneer plant (Rønning, 1979; Korsager et al. 2003).

How important vascular plants were for primary soil development is not known. Present day studies in Svalbard have shown that the highest flux of biologically fixed nitrogen comes from free living colonies of cyanobacteria in wet sparsely vegetated ground, or as epiphytes on bryophytes. In contrast, vascular plants were found to be insignificant in fixing nitrogen in this environment (Solheim et al. 1996). It is possible that there was a pioneer phase of cyanobacteria stabilising and fertilizing the ground before the first plants colonised. Evidence for this scenario was found at Usselo (Netherlands) (van Geel et al. 1989, van Geel et al. 1996).

#### 5.2.2. Bølling: (SL-2) 14,700 cal yr BP – 14,100 cal yr BP

At the onset of the Bølling warming *B. nana*, *Dryas octopetala* and *Salix* sp. pollen percentages increased together with macrofossil concentrations and pollen accumulation rates. The vegetation during this period in the Danish area is, apart from Slotseng, only known through a few records of *S. polaris* (Korsager et al. 2003), but records from northern Germany and The Netherlands suggest that the landscape was then dominated by a heliophilous herbaceous vegetation (e.g. Hoek, 2001, de Klerk, 2002; Bos et al. 2006).

The onset of the Bølling warming prompted a response in all proxies, starting with a rapid increase in *Pediastrum boryanum* in the lake. The increased sediment accumulation rate may have resulted from permafrost melting and releasing material that was washed into the lake. The high pollen accumulation rate may be associated with slumping or changes in sediment focusing caused by modifications in basin morphometry as dead ice beneath the lake floor melted. These impacts on the sedimentary system seem to last through the Bølling and Older Dryas periods (Mortensen, 2007). However, despite this disturbance within the lake the stratigraphy of sediments at the location where the monoliths were collected seems to be unaffected.

In the lake the rapid increase in *P. boryanum* is followed by an increased diversity in the aquatic plant community with the presence or increase of pioneer taxa such as *Potamogeton filiformis*, *Ranunculus* subgen. *Batrachium*, *Hippuris vulgaris*, *Chara* sp., *Myriophyllum spicatum*, and *M. verticillatum*, *Fontinalis* sp., *Nuphar*, and the deep-water *P. praelongus*. Telmatic vegetation containing *Potentilla palustris*, *Juncus*, and *Carex* spp grew at the lake shore and *Parnassia palustris* was present, perhaps accompanied by *Saxifraga hirculus* in base-rich flushes. By the end of the Bølling period several of the submerged plants seem to have disappeared. This might be associated with internal disturbances in the lake such as displacement of sediment due to slumping and melting of dead ice causing the depositional floor to sink (Mortensen, 2007) leading to water turbidity.

The local upland vegetation developed into an open dwarf-shrub community dominated by *B. nana*, *Helianthemum oelandicum*, *Salix*, and *D. octopetala* together with Poaceae, and scattered amounts of *Minuartia* cf. *rubella*, *Sagina intermedia*, *Draba* sp., and the steppe species *Gypsophila fastigiata* (macrofossils), and *Astragalus alpinus*, *T. alpinum* and *P. maritima* (pollen), all species tolerant of soil disturbance, as reflected by high SUS and low LOI and of low soil nitrogen (Fig. 7). The typical habitat of *D. octopetala* is dry, open and exposed places, often on base-rich soils, where it tolerates some disturbance and limited snow cover. All the *Dryas* leaves recorded are of the type adapted to wind exposure (Bennike, 1987) indicating that the area was relatively open and wind exposed. *B. nana* is more commonly found in damp and boggy areas, but it can be associated with *Dryas*, for example in northern Sweden today. On Svalbard, *S. polaris* and *Dryas* form a widespread vegetation type in the coastal zone (Rønning, 1979). Pollen percentages of *Hippophaë rhamnoides* show a double peak, which is characteristic of the Bølling period in Schleswig-Holstein (Usinger, 1998). Since *Hippophaë* is insect pollinated with low pollen production it is likely that this shrub was present locally, although not as abundant as reflected by the pollen records from northern Germany (Usinger, 1985, 1998, de Klerk, 2004).

Besides high stress tolerances, the ability to form symbiosis with N-fixing bacteria may have been a factor in the survival of the pioneer taxa. This ability is a common characteristic for many of the late glacial taxa recorded in Slotseng such as *Lotus* and *Astragalus*, *Hippophaë rhamnoides*, *Dryas octopetala*, *Silene acaulis*, and different species of *Salix* and *Poaceae* (e.g. Lifshitz et al. 1986; Harrington and Mitchell, 2002).

While several relatively thermophilous species are recorded in the pollen assemblages (e.g. tree birch, *Hippophaë*), the macrofossil assemblages are dominated by arctic plants.

Fair amounts of pollen of tree birch, Dryas, *P. maritima, Helianthemum oelandicum* t. *etc*. might indicate a "non analogue" situation during the first phase of the late glacial. In contrast, the macrofossil assemblages suggest a relatively close analogue to the low and mid alpine vegetation in the Scandinavian mountain region today, for example in the Abisko area of North Sweden, but a closer look suggests some support for the presence of non-analogue communities. Apart from a few relict occurrences on calcareous soil in Scandinavia *Gypsophila fastigiata* has its present distribution in East and Central Europe (Hultén and Fries, 1986;

Mossberg et al., 1994). *G. detonsa* occurred in the early Allerød, and with its present European distribution confined to usually salt-affected communities in Iceland and Norway, is also an atypical element in present-day analogues from Scandinavia.

*5.2.3. Older Dryas: (SL-3) 14,100 cal yr BP – 14,000 cal yr BP*

Although zone SL-3 was delimited as significant, the responses to any climate change during the Older Dryas at Slotseng are slight and not synchronous in the records of the different environmental proxies. In the pollen percentages the onset of the Older Dryas may be indicated by a percentage decrease in *B. nana* type (but not its influx) and a marked increase of *H. oelandicum* type at approximately 14,100 cal yr BP. Within the lake system a decrease in LOI dated to approximately 14,050 cal yr BP may be a response to the transition. On dry land an increase of drought tolerant species (e.g. *Campanula* cf. *rotundifolia*, *G. detonsa*, *Rumex acetosella*, *Lychnis alpina*) in the macrofossil assemblage at approximately 14,000 cal yr BP may be interpreted as a climatic response. If these changes reflect the same climatic event there is a time-transgressive response of about hundred years within proxies from the same site. The estimated age of 14,100 cal yr BP for the onset of the Older Dryas seems to compare well to that of other studies. From northern Germany a decrease in *Betula* pollen has been estimated to 14,000 cal yr BP (de Klerk, 2004), and in The Netherlands to 14,100 cal yr BP (Hoek, 2001).

The diversity of aquatic macrophytes is reduced in this phase. Macrofossils of *Potamogeton filiformis*, *Chara* sp., *Ranunculus* subgen. *Batrachium*. and pollen of *Myriophyllum spicatum* and *Sparganium* t. are the only aquatic remains recorded. A temporary decrease of LOI may reflect a lowering of the lake level and erosion of minerogenic material from the lake margin (Mortensen, 2007). Alternatively, it may reflect reduced lake productivity or the increase of aeolian deposition in a drier climate. Disturbed conditions may have resulted in the increased numbers of *Daphnia* ephippia. The marginal vegetation remained unchanged, but the presence of cold permanent flushes and damp basic grassland, perhaps related to snow-beds, are shown by the occurrence of *Koenigia islandica*, *Saxifraga aizoides* t., and *Selaginella selaginoides*.

The upland vegetation during the Older Dryas and early Allerød seems to have become more open, with increased amounts of *Helianthemum* spp, Poaceae, and of many light demanding and drought tolerant taxa such as *H. oelandicum*, *Matricaria* t., *G. fastigiata*, *Silene acaulis*, *Campanula* cf. *rotundifolia*, *Campanula trachelium* t., *Artemisia*, and *Rumex acetosella*, many of which prefer dry and often basic soil. The double peak in pollen percentages of *Helianthemum* is characteristic of the Older Dryas in this region (Usinger, 1985, 1998; Mortensen, 2007). The relatively high percentages of *Helianthemum* (up to 8%) suggest that it grew in the vicinity of the lake although no macrofossils have been found. *B. nana* type, *Dryas*, and *Hippophaë* show no decrease in pollen accumulation rates or in macrofossil concentrations. This suggests that the pollen percentage decline of these taxa is the result of the increase in Poaceae percentages, resulting from a large increase in its influx.

The Older Dryas is recorded as a temperature decrease in the Greenland isotopic records (Rasmussen *et al.*, 2006). However, the nature of the Older Dryas climatic event in North Central Europe is difficult to interpret from pollen records. Some records are interpreted as an indication of a cooling (e.g. Iversen, 1954; Usinger, 1985, de Klerk *et al.*, 2001) and others as a period of drought (e.g. Kolstrup, 1982; Berglund *et al.* 1994). At Slotseng, the generally increasing pollen accumulation rates and the stability of the macrofossil assemblages do not indicate a deterioration of growth conditions during the Older Dryas and early Allerød and there are also no suggestions of a major reduction in the vegetation cover. Rather, there are increasing concentrations of macrofossils of species associated with dry conditions, e.g.: *S. acaulis*, *Campanula* cf. *rotundifolia*, *R. acetosella*, *G. detonsa*, and *Lychnis alpina*, while there is a reduction in arctic species. In the pollen record upland species such as *H. oelandicum*, *Campanula trachelium* t., *R. acetosella* t., and *Artemisia* increased. The record of several seeds of *G. detonsa* is worth emphasising because of its ability to tolerate saline soil. In Greenland today, *G. detonsa* grows in continental areas where high evaporation causes elevated salt concentrations in the soil and, according to Böcher (1954, 2000), is an indicator of "low arctic salt steppe". *G. detonsa*, together with the assemblage of other drought-tolerant species, is a good indicator of locally more dry conditions during the late Bølling to early Allerød. A period of drought is also indicated by the lake level that seems to decrease temporarily during the Older Dryas (Mortensen, 2007).

*5.2.4. Allerød 1: (SL-4) 14,000 cal yr BP – 13,600 cal yr BP*

The transition from the Older Dryas to the Allerød is neither detectable in the aquatic and wetland communities nor in the SUS measurements. LOI values, however, increased, suggesting increased productivity and landscape stabilisation. The macrophytes were still *Chara*, *Ranunculus* subgen. *Batrachium*, and *Potamogeton pusillus* t. *Botryococcus* increased whereas *Pediastrum* decreased. During this zone *Cristatella mucedo* was present in the lake and increased towards the end of the zone, suggesting an increase in lake-water temperature (Økland and Økland, 2000). The fen vegetation was developing with *Potentilla palustris* and *Carex* spp. as dominants. Some moist flushes supported *Selaginella selaginoides*, *Saxifraga aizoides*, and *Thalictrum alpinum*, although *Koenigia* was no longer recorded.

The transition to the Allerød is marked in the terrestrial assemblage by an abrupt decrease in *D. octopetala* pollen and macrofossils and more gradual declines of *B. nana* pollen and macrofossils and *H. oelandicum* pollen. At the same time, *Salix* remains and pollen percentages increased markedly, but *Salix* pollen influx remained more or less constant. Poaceae macrofossils show a similar abrupt increase. Its pollen percentages are as high as before, but its influx decreased slightly. These records are interpreted as an expansion of more closed vegetation dominated by *Salix* and grasses. However, many herbs of dry open habitats persisted, shown by macrofossils and pollen, that previously characterised the Older Dryas, with particularly large amounts of *Campanula rotundifolia*, *Rumex acetosella*, and *G. detonsa* and the addition of *Luzula* and *Potentilla nivea* t. The changes are reflected in the gradual increases in DCA axis 1 values for both pollen and macrofossils. This *Salix*-Poaceae dominated assemblage existed for approximately 400 years until the first tree-birch macrofossils were recorded at the end of the zone, probably reflecting colonisation of damp sites near the lake margin.

*5.2.5. Allerød 2: (SL-5) 13,600 cal yr BP – 13,150 cal yr BP*

During this period the macrophyte vegetation of *Potamogeton alpinus*, *P. pusillus* t., *P. vaginatus*, *Nitella*, and *Chara* became overgrown by a mat of *Drepanocladus exannulatus* and *Sphagnum* sect. *Squarrosa* with abundant *Carex* cf. *rostrata* associated with fen herbs such as *L. europaeus* and *Epilobium*. Open water was reduced to small pools that supported *Myriophyllum* spp and *Sparganium* t. This hydroseral development can be followed in the lithology as a gradual development from gyttja to moss peat with decreasing inorganic content. The moss peat and the development of telmatic vegetation surrounding the lake created a separation barrier that effectively filtered out most of the in-washed material and prevented it from reaching the centre of the basin. This process reduced the diversity in the macrofossil assemblage, now being

dominated by the taxa growing on or very close to the basin. The resulting reducted pollen influx is therefore not comparable to the influx in previous zones as in-washed pollen was no longer contributing to the total. The marked decrease observed in the accumulation rates of *Betula* spp pollen is, therefore, most likely not an effect of a decrease in the *Betula* population or in *Betula* pollen production but rather a result of the changes in the sedimentary environment.

An outstanding characteristic of zone SL-5 is the first appearance of macrofossils of tree birch in high abundance. Tree birch was locally present, probably growing on the moist soils around the basin. Fruits of *B. nana* are also still well represented and leaves were recorded, suggesting that *B. nana* was growing locally on drier peaty habitats at the edge of the basin as well as on drier slopes of the catchment, perhaps with *Juniperus*. Macrofossils of *Arctostaphylos alpinus* in this and the following phase Allerød 3 may also be an indication that vegetation was still open in the catchment. The DCA axis 1 scores of pollen and plant macrofossils reflect the increase of shade tolerant species from mid Allerød through to the onset of the Younger Dryas (Fig. 7). However, during the Allerød shade tolerant species never became as dominant as during the Preboreal, shown clearly by the DCA scores (Fig. 7).

#### 5.2.6. Allerød 3: (SL-6/Gerzensee oscillation) 13,150 cal yr BP – 12,950 cal yr BP

During this short period the basin was covered by a fen dominated by the mosses *D. exannulatus*, *Sphagnum* sect. *Squarrosa*, and *Carex* cf. *rostrata*. Besides these taxa evidence regarding local vegetation is poor. Tree birch, *B. nana*, and *Salix* were still present but are poorly represented in the macrofossil assemblages and they have much reduced pollen influx, although there is a peak in tree-*Betula* t. pollen percentages. Whether this reflects a true reduction in their local presence caused by the cooler climate of the Gerzensee oscillation (Eicher and Siegenthaler, 1976) or a reduced deposition caused by sedimentary changes cannot be determined. The main characteristic of the Gerzensee oscillation in pollen diagrams from Denmark is described as a minimum in *Betula* pollen and maxima in *Pinus* and herb pollen (Andersen *et al.* 2000). *Pinus* percentages increase in Slotseng, whereas the influx values remain low. This may be caused by reduced pollen production due to cooler conditions thereby enhancing the relative importance of long distance transported pollen e.g. *Pinus* in the percentage diagrams.

#### 5.2.7. Allerød 4: (SL-7) 12,950 cal yr BP – 12,800 (?) cal yr BP

There are no indications of changes in the local vegetation development in this zone except for a huge peak of *Carex* cf. *rostrata* fruits (>500 seeds pr. 100 ml). An increase in *Betula nana* pollen might indicate a warming after the Gerzensee oscillation. However, the fossil record is likely to be affected by an assumed short hiatus between this and the following zone. The increase in *B. nana* pollen could therefore be caused by erosion and mixing during the early part of the Younger Dryas. This is also indicated by the decrease in LOI in the upper part of the zone.

#### 5.2.8. Younger Dryas: (SL-8) 12,800 (?) cal yr BP – 11,500 cal yr BP

The Younger Dryas represents a cold period when the water-level rose and the basin once more became a lake due to less evaporation, vegetational changes in the catchment area, and perhaps increased precipitation (Bohncke, 1993; Magny and Ruffaldi, 1995). Erosion of sediment into the basin may have compacted the *Sphagnum/Drepanocladus* mat. It is likely that this process resulted in a slight erosion of the peat surface so that there is a hiatus in the series at the peat/limnic sediment transition (see Mortensen, 2007). The aquatic vegetation documented is sparse and furthermore the fossil record may be affected by redeposition of older material eroded from the Allerød peat near the lake margin. Small clasts of redeposited peat and organic material from the Allerød layers were found embedded in the lower Younger Dryas sediment (Mortensen, 2007). Tall fen vegetation persisted, composed of *Carex* spp., *Juncus*, and *Equisetum*, and later, *Ranunculus flammula*. Later, mossy mires developed perhaps with *Sphagnum* and *Paludella squarrosa*, and with *Selaginella* and *Parnassia*. Towards the end of the Younger Dryas the lake system became more stable and an aquatic vegetation of *Nitella*, *Chara*, *Myriophyllum spp*, *Potamogeton alpinus*, *P. pusillus t.*, *Ranunculus* subgen., *Batrachium*, and *H. vulgaris* developed. *Cristatella* statoblasts occurred throughout the Younger Dryas, indicating that temperature conditions were not more severe than about 10 °C mean July temperature (Økland and Økland, 2000).

The record of terrestrial plant communities differs from that of earlier cold stages but seems slightly confused by rebedded fossils. The few macrofossils of tree birch found in the Younger Dryas layers are likely to be rebedded from the Allerød peat rather than primary fossils from locally surviving birch trees. Increased soil instability and erosion during the Younger Dryas is shown by the low LOI percentages and by the record of *Cenococcum geophilum* sclerotia that were washed in with the soil. *B. nana* and *Salix* sp. were common in the catchment. The upland vegetation furthermore appears to have been relatively diverse with *P. nivea* being very common. This species as well as many of the other taxa recorded (*Androsace septentrionalis*, *Campanula* cf. *rotundifolia*, *Dryas octopetala*, *Gypsophila* cf. *fastigiata*, *L. alpina*) prefer dry calcareous soil. Though climate became cooler, few of the arctic species found in the pre-Bølling and Bølling periods reappeared. Thus, *Dryas octopetala*, an important plant during the early Lateglacial is rather insignificant in the Younger Dryas. The arctic-alpine species were excluded by Allerød birch-woodland development and they persisted near the margins of the ice sheet (Birks, 2008). They had insufficient time to return to Denmark during the Younger Dryas, which in any case was not particularly cold and allowed the expansion of more thermophilous and competitive species of open habitats. During the late Younger Dryas an increase in *Empetrum* is a recognized widespread feature of the Northwest European region having been associated with increased aeolian activity and leached soils (Hoek, 1997). At Slotseng *Empetrum* seeds occurred locally near the Younger Dryas/Holocene transition but its pollen percentages did not increase until the early Preboreal when the catchment became more stabilized. There is no evidence in the sediment of permafrost movements as in The Netherlands.

#### 5.2.9. Preboreal 1: (SL-9) 11,500 cal yr BP – 11,300 cal yr BP

With the Holocene warming the lake was rapidly overgrown by a fen of *Carex* cf. *rostrata*, *Potentilla palustris*, *Filipendula*, *Sphagnum*, and *Drepanocladus*. Also *Eriophorum vaginatum* and *E. angustifolium* were present in the upper part of this zone as part of the wet acid mire. The peat was almost 100% organic. In one sample containing >200 pr. seeds of *Carex* cf. *rostrata* pr. 100 ml 10–15% were carbonized or partly carbonized and much charcoal was present on the pollen slides, showing that the wetland area had been burned. It is impossible to decide whether this fire was natural or caused by early Mesolithic human activity. The increase in the rate-of-change of pollen assemblages reflects the rapid replacement of *B. nana* and *Salix* vegetation by *Juniperus communis* and *Empetrum*.

#### 5.2.10. Preboreal 2: (SL-10) 11,300 cal yr BP – 10,800 cal yr BP

The development of birch forest at Slotseng was delayed by 200–250 years compared to the northwest European mainland (e.g. Hoek, 2001, de Klerk, 2002) where tree birch spread rapidly at

the beginning of the Holocene. The delayed expansion at Slotseng suggests that tree birch probably did not survive locally during the Younger Dryas. An alternative hypothesis is that erosion and solifluction of the Younger Dryas had made soils less suitable for the establishment of tree birch and hence slowed down its expansion in the Preboreal. Tree birch arrival is reflected by very high macrofossil concentrations and pollen percentages and influx, a marked decrease in palynological evenness, a high rate-of-change, and in the significant explanatory power of tree-birch macrofossils for the variance in the pollen data (Fig. 8). *Carex* cf *rostrata* and the mosses disappeared from the basin mire which became dominated by *E. vaginatum*, *E. angustifolium*, and *Potentilla palustris* with possibly some *Nymphaea alba* in pools. The surrounding area was covered by open woodland composed of *Betula pubescens* and *Populus tremula* that replaced the dwarf-shrubs and herbs and *Salix*. At the end of the zone, trunks and branches of *Pinus* in the sediment show that pine grew on the mire surface. There is only a small increase in its pollen percentages but its influx is high, suggesting that the large amounts of *Betula* pollen had reduced its percentage representation.

#### 5.2.11. Late-glacial forest development

Based on pollen evidence it has been argued that tree birch migrated to the Danish area and southern Scandinavia as early as the Bølling period (e.g. Iversen, 1954; Kolstrup, 1982; Paus, 1995; Noe-Nygaard *et al*. 2006). However, the alleged presence of tree birch in Denmark during this period rests on evidence from the pollen record from Lake Bølling (Iversen, 1942, 1954) the age of which is difficult to interpret (Bennike *et al*. 2004a; Mortensen, 2007) and from studies lacking $^{14}$C determinations (Kolstrup, 1982). Because of the difficulties in distinguishing between local and background (long distance transported) pollen sources, the presence of tree-birch macrofossils is a far more reliable indication of local occurrences than pollen records are. Pollen distribution maps from the late glacial (Huntley and Birks, 1983) suggest that *Betula* migrated largely from the east, making an earlier occurrence on Zealand likely. However, no macrofossil studies from east Denmark date back to the early late glacial and the earliest documented macrofossils of tree birch belong to the Allerød period (Hartz and Milthers, 1901; Jessen, 1920; Usinger, 1977; Bennike and Jensen, 1995). In western Skåne (southern Sweden), one macrofossil record indicated that tree birch may have immigrated already during the Bølling period (Jönsson, 1988). However, since this record relies on dating of bulk sediment samples with low organic content its age is uncertain. Local presence of tree birch should not be definitively inferred from a single macrofossil (Birks and Bjune 2010). Therefore, no unequivocal documentation exists of tree birch migration into southern Scandinavia during the Bølling period. In western Denmark the local occurrence of tree birch may have been further delayed. Tree birch was not present at Slotseng until the mid Allerød (13,600 cal BP). At Lake Bølling (Fig. 1) macrofossil analyses indicate that tree birch may not even have arrived until the Preboreal (Brandt, 1954; Stockmarr, 1975; Usinger, 1985; Bennike *et al*. 2004a). It is likely that the delayed spreading of tree birch was caused by lack of suitable soils, since temperature reconstructions from the Bølling period indicate temperatures well above the lower growth limit of tree birch (e.g. Renssen and Isarin, 2001). Although *B. pubescens* and *Betula pendula* are tolerant of severe winter cold, both are sensitive to summer drought (Nikolov and Helmisaari, 1992).

The inferred relatively open vegetation at Slotseng during the Allerød period contrasts to the classical interpretations of this period as having an open birch 'park-tundra' during the early Allerød, followed by a relatively dense birch woodland in the late Allerød (e.g. Iversen, 1954, 1973; Noe-Nygaard *et al*. 2006). Was the late glacial "forest" at Slotseng a mere local development or was it representative for the development in a larger area? Quite a number of pollen based studies do indicate that the Danish Allerød birch forest had a mosaic-like vegetation structure (Jessen, 1920; Andersen, 1980; Kolstrup, 1982; Kolstrup and Buchardt, 1982; Kolstrup, 1999; Bennike *et al*. 2004b). This interpretation is supported by macrofossil evidence of *Arctostaphylos alpinus* and *B. nana* found together with tree birch (Hartz and Milthers, 1901; Jessen, 1920; Bennike *et al*. 2004b, this study). Furthermore, documented aeolian activity during the Allerød period indicates a more patchy development of the vegetation particularly in West Denmark (Kolstrup, 2007). Such evidence points to the existence of a heterogeneous vegetation cover during the Allerød period varying from very open herb and dwarf-shrub dominated communities to rather dense birch forest.

*Pinus* has traditionally been considered a part of the Allerød birch-forest vegetation in Denmark (Iversen, 1954). Though the pollen percentages for *Pinus* might be taken as evidence of local growth (Lang, 1994) during the late Allerød, no macro-remains have been recovered from the Danish area until the Preboreal (Bennike et al., 2004b). Also, available pollen accumulation rate data show no Allerød *Pinus* peak and consequently the *Pinus* percentage pollen peak of this period is probably caused by a relative reduction in local pollen production during the cool Gerzensee oscillation. The oldest documented occurrence so far of *Pinus* in Denmark is based on megafossils from a submerged *Pinus* forest in the Great Belt of the Baltic Sea dated to 10,100 cal yr BP (Fischer, 1997) but the Slotseng record now pushes the earliest presence of *Pinus* back to 10,800 cal yr BP. The oldest macrofossils of *Pinus* in neighbouring areas are from the Younger Dryas–Holocene transition ($\sim$10000 $^{14}$C yrs BP BP, southern Sweden, Jönsson, 1988) and from the Younger Dryas (10540 $\pm$ 120 $^{14}$C yrs BP BP, northern Germany, Bennike and Jensen, 1998). One exception to this pattern is a remarkable find of carbonized *Pinus* wood from an archaeological excavation in Schleswig-Holstein radiocarbon-dated to 12200 $\pm$ 60 $^{14}$C yrs BP (Clausen, 1998) and palynologically correlated to the late Bølling (Meiendorf) period (Usinger, 1998). This might indicate a much earlier spread of *Pinus* than previously assumed, but with the connection to a palaeolithic settlement, human influence cannot be excluded. Wood was a valuable resource in an (almost?) treeless landscape and could have been brought to the settlement from a long distance or collected as driftwood in rivers such as the Elbe. If they are locally sourced, the *Pinus* occurrences in Schleswig-Holstein indicate that *Pinus* could have been a local element of the late-glacial flora in Denmark. So far, the only taller woody plants recorded as macrofossils from the Lateglacial period in western Denmark, are tree birch and *Populus* (Nielsen and Sørensen, 1992; Mortensen unpublished data). From eastern Denmark additional taxa have been recorded as macrofossils; *Juniperus* (Hartz and Milthers, 1901; Jessen, 1920; Mortensen unpublished data), *Hippophaë* (Mortensen unpublished data), and *Salix* cf. *caprea* (Iversen, 1954; Mortensen unpublished data). The presence of *Sorbus* in several pollen assemblages indicates that it may also have been a natural element of the late-glacial "forest" (Iversen, 1954; Mortensen unpublished data).

The above discussion challenges the classical interpretation of the Lateglacial forest development in Denmark. It is proposed that the expansion of tree birch was delayed mainly by the lack of suitable soils and aridity during the early part of the late glacial. Not until the Allerød period did tree birch spread, and then presumably through the wetland areas while drier and more exposed habitats with raw soils remained treeless. It is also likely that large parts of western Jutland remained treeless until the early Holocene. While *Juniperus* has a documented presence in the vegetation in eastern

Denmark during the Allerød, *Pinus* could potentially have occurred locally in southeast Denmark during this period.

Though Slotseng is a small-scale site which primarily reflects the local environmental changes, most of the variations in the pollen assemblages compare well to known biostratigraphical phases in the region. The first phases especially, with pioneer vegetation development, seem to be identical to those in continental north-western Europe and therefore probably reflect synchronous responses to the large-scale climate warming. Therefore it is evident the SL-2 belongs to the first late-glacial warm stage. This is also supported by the chronology from the site. The Slotseng site thereby provides the first unequivocal palaeoecological record for the early late-glacial warming in Denmark.

## 6. Conclusions

The Slotseng stratigraphy covers more than 5000 years of late glacial and early postglacial vegetation development. The small basin is a kettle hole and the earliest deposits are affected by buried ice-melting. The small lake gradually became filled by sediment as aquatic vegetation developed and organic material was also supplied from the catchment soils. At the end of the Allerød period, it was covered by a moss carpet of *Sphagnum* and *Drepanocladus*. At the start of the Younger Dryas, lacustrine conditions were renewed, but by the start of the Holocene, the lake once more became overgrown by a sedge fen and shrubs, and eventually supported pine trees.

Slotseng is the first Danish site with a bio- and chronostratigraphy that unambiguously reflects the environment of the earliest late glacial, the Bølling period. Reconstruction from pollen and macrofossil data shows that the vegetation of the Bølling and Older Dryas periods around Slotseng was dominated by *B. nana* and *D. octopetala* associated with many herbs of open habitats. The most important limiting factors for the vegetation development during these phases were probably soil instability, aridity, and low soil nitrogen rather than low temperature. The early late-glacial local vegetation was a mixture of arctic-alpine and steppe elements with no direct modern analogue. Increasing numbers of macrofossils from drought-tolerant species indicate increased aridity during the Older Dryas and early Allerød periods.

With the onset of the Allerød the vegetation contained increased amounts of *Salix* and grasses. This vegetation type remained for approximately 400 years until the mid Allerød when the first tree birches began to grow locally. The first axis of a DCA of the pollen data, as well as records of evenness, rate-of-change, and macrofossil assemblages, indicate a distinct contrast in the vegetation succession between the Allerød and Preboreal forest phases. During the Allerød tree-birch vegetation was most likely restricted to the moist soils near the basin while the drier areas remained treeless. Indications from earlier studies show that this vegetation structure might have been the general pattern during the Allerød period in Denmark albeit with increasingly more open conditions towards the west. With the onset of the Younger Dryas cooling, soil instability and erosion increased and the Allerød vegetation was replaced by a new phase of pioneer vegetation. With the Holocene warming, the vegetation became dominated by *J. communis* and *Empetrum*. This phase lasted approximately 200–250 years before birch forest covered the area. The local pollen assemblage zones at Slotseng can be biostratigraphically correlated to the major phases known from the region.

The combined use of macrofossil and pollen records in reconstructions of late-glacial environments allows deeper insights into the vegetation and environmental development. More such integrated studies are needed in order to test earlier conclusions on the late-glacial environmental development in Denmark and if the Slotseng record is entirely local or has a wider applicability.

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## Supplementary material

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